

Behavior and Nesting Dynamics of the Neotropical Cavity-nesting Specialist Bee *Megachile assumptionis* Schrottky, with Comparisons to the Nearctic *Megachile brevis* Say (Hymenoptera: Megachilidae)

DANIELA A. O. ALMEIDA, ROGERIO PARENTONI MARTINS, AND MARIA LUÍSA T. BUSCHINI

Laboratório de Ecologia e Comportamento de Insetos, Dep. Biologia Geral-ICB/UFMG,
Caixa Postal-486, 30161-970, Belo Horizonte, MG, Brazil

Abstract.—We describe the behavior and nesting dynamics of the solitary leaf-cutter bee *Megachile assumptionis* Schrottky, which nests exclusively in deserted burrows of the solitary apid bee, *Ptilothrix plumata* Smith. Adults were active between April and September. Males patrolled the nesting sites and flowering bushes searching for females and nectar. Mating occurred both on the soil near the nests and on flowers of *Vernonia rubriramea* (Asteraceae). Females only investigated and selected single-celled deserted nests on trails where *P. plumata* had previously nested. The nest is a vertical burrow in which the walls are lined by the females. The brood cell is linked to the outside by a tunnel filled with leaf fragments. Two caps of masticated leaves close the nest tunnel at different levels and another closes the cell. The nests were supplied with provisions of pollen and nectar and the females laid their eggs on the top of a semisolid provision mass. Adults emerged at different times of the year, which suggests that there are at least two annual generations. Prepupae of *M. assumptionis* can remain dormant in the cells either from October to March or from April to August. The nesting biology of *M. assumptionis* differs from that of the Nearctic *Megachile brevis* Say, particularly in the latter's use of several kinds of cavities and in the comparatively greater abundance and mobility of the individuals.

While the majority of bees are solitary, constructing their nests in bare, drained ground exposed to sunlight (Batra 1984; Martins and Antonini 1994; Martins *et al.* 1996), the family Megachilidae shows a wide range of nesting types, including species that construct free-standing nests, many that nest in the soil, and others that dig their nests in wood or plant stalks or even occupy pre-existing cavities (Michener and Szent-Ivany 1960; Krombein 1967; Bohart and Youssef 1972; Eickwort *et al.* 1981; Martins and Almeida 1994). The Megachilidae are also biologically interesting in the way they draw on a wide variety of material in constructing their nests, such as cut pieces of leaves and petals, chewed leaves, plant fibers, resin, clay, mud, sand, and pebbles (Stephen *et al.* 1969; Yanega 1994). Two other unusual features, not found in the parasitic species

of this group, are the method of transporting pollen on a ventral abdominal scopa (rather than pollen-gathering hairs on the legs) and the practice of cutting pieces of leaves in constructing nests (in species of the genus *Megachile*, from which the name "leaf-cutter bees" is derived; Stephen *et al.* 1969; Michener 1974).

Megachile that nest in pre-existing cavities show differing degrees of specialization, ranging from those that nest exclusively in the empty shells of molluscs, termite nests, or deserted nests of another solitary bee species to those that use a wide variety of cavities (Michener 1953; Stephen *et al.* 1969; Iwata 1976; Messer 1984; Martins and Almeida 1994). The habit of using pre-existing cavities apparently has evolved, several times, from digging ancestors (Eickwort *et al.* 1981).

M. assumptionis Schrottky is at one end

of this specialization ranking, as it nests exclusively in the deserted nests of another solitary bee, in the family Apidae (=Anthophoridae), *Ptilothrix plumata* Smith. This may result either from adaptation or preadaptation and could have an influence on the ecological characteristics of the species, such as a limit to population growth (Martins and Almeida 1994).

Unfortunately, there has been a scarcity of detailed studies into the ecology and behavior of solitary bees in the Neotropics (Roubik 1989, but see Martins and Antonini 1994; Martins and Almeida 1994; Martins and Figueira 1992; Martins *et al.* 1996). In Brazil, despite the great richness of *Megachile* species (Sakagami *et al.* 1967), displaying remarkable interactions in complex and varied environments, the lack of studies has meant that knowledge of these insects is limited.

The aim of our study was to provide information on the nesting behavior and dynamics of *M. assumptionis* from the foundation of the nests to their closure, and later on, emergence of the new adults. A further objective was to compare the biology of *M. assumptionis* with that of *M. brevis*, a well-studied species in the Nearctic region (Michener 1953).

METHODS

The work was undertaken in the Ecological Station of the Campus-Pampulha of the Universidade Federal de Minas Gerais, Belo Horizonte, Brazil. This station comprises 156 ha of mixed vegetation, which is crossed by a number of trails and dirt roads, as described in Martins and Almeida (1994). Preliminary observations relating to *M. assumptionis* and its interactions with *P. plumata* were made in May 1992 but most of the present data was obtained from January 1993 to September 1994, totalling 485 hours of observation (225 and 260 hours, respectively).

The *ad libitum* and "focal individual" methods were used to study nesting behavior (Martin and Bateson 1993). A 700m

trail was visited between 0900 and 1300 hours, the peak hours of bee nesting activity. From April to September visits were more frequent (at least 10 days per month). From October to March visits were more sporadic as there is usually no adult activity in this period; only routine checks were required to see whether new individuals had emerged.

We analyzed selection of nesting site, cell construction, provisioning, nest closure, mating, male patrolling, longevity and adult mobility. Captured individuals had their scutum marked with fast-drying paint. If recaptured, they were recorded, remarked if necessary, and released again.

Nesting dynamics were studied by recording every single *P. plumata* and *M. assumptionis* nest along the same trail. The nests were identified and labelled with metallic arrows (4 cm long by 5 mm wide) nailed to the ground. The arrows were either distinguished by different colours corresponding to those colours marked on their respective founding females or else marked by numbers. After the nests had been closed by the females, marked plastic cup emergence traps were nailed over the entrances to record the period of egg-adult development and emergence of brood parasites.

Twenty-three nests were excavated in 1993 and 10 in 1994 in order to study their inner structures, the material used in their construction, and the development of the immature stages. The method of determining the degrees to which water would penetrate a cell was to submerge it in water for 24 hours.

We measured height and width of six cells and tunnels and calculated average and standard deviation for all these measurements. Voucher specimens of the bee species were deposited at the Laboratório de Ecologia e Comportamento de Insetos of the Departamento de Biologia Geral, ICB-UFMG, Belo Horizonte, Minas Gerais, Brazil. Two *M. assumptionis* females were also deposited in the Snow Entomological

Museum of the University of Kansas, Lawrence, KS, USA.

RESULTS AND DISCUSSION

Nesting Site Selection and Cavity Occupation.—The main factor which constrains the nesting behavior of *M. assumptionis* is the availability of *P. plumata* nests, as the former species nests exclusively in deserted nests of the latter (Martins and Almeida 1994). No females were observed either digging or nesting in any sort of potentially suitable cavities such as crevices in the soil and sand banks, termite burrows, or vacant nests of *Diadasina distincta* Holmberg (Apidae); all of these are used, for example, by *M. neoxanthoptera* Cockerell, another syntopic and cavity-generalist megachilid (Martins and Almeida 1994; Martins and Antonini 1994).

Females of *P. plumata* adopt a scattered-nesting behavior which influences the searching behavior of *M. assumptionis* females. They fly over the area and select one from a number of potentially available nests. The searching flight itself and the exact moment of selection was not observed, but the females would explore cavities and decide about its occupation by flying in a sinuous or zigzag course, close to the ground, investigating sticks and other possible nesting places, in the same way as females of *M. brevis*. The flight is continuous apart from irregular and often rather long interruptions which occur while a bee crawls into a hole (Michener 1953). The precise factors that determine whether or not *M. assumptionis* and *M. brevis* females will decide to occupy a cavity are presently unknown.

Only one kind of flight has been recognized as characteristic of *M. assumptionis* females. This flight helped to distinguish females from males (see below). It was a fast flight, about 50 cm above the ground, along the trail, without any pause for an investigation of cavities. One explanation for this flight might be that it is associated with the nest-provisioning phase.

There were two cases of reoccupation of *M. assumptionis* nests, from which adults had already emerged, apart from the occupation of deserted nests of *P. plumata*. These nests were reoccupied by other females, 2–7 days after their emergence. Nest reoccupation was not observed for *M. brevis* (Michener 1953).

The females and males have also been seen inside either deserted or active nests of *P. plumata* and even in other shallower and narrower cavities (between 1–2 cm). In these cavities, the individuals often stayed for an undefined period (from a few minutes to one hour) or even stayed overnight, with the abdomen visibly raised, close to the nest entrance. There is no evidence that either the males or the females spend the night inside their own nests, or those of conspecifics. However, *M. brevis* females spend the night in their nests and also probably hiding in curled leaves or seeking similar protection (Michener 1953). Females of *M. assumptionis* may, however, remain in the nest during strong rains. This was observed for a female that was coming back from a provisioning trip. She entered the nest tail-first and remained there with her head close to the nest entrance. When the rain had started, she exited and re-entered the nest, head first, keeping her abdomen up (the only visible part) and blocking the nest entrance. At the same time, two females of *P. plumata* were in a similar position in their own nests, next to the *M. assumptionis* nest; this behavior might be attributed to the need to protect provisions from rain water and was not observed in *M. brevis*.

Male Patrolling Behavior.—The males were normally seen patrolling the nesting site. They fly just above the ground, investigating a variety of cavities, such as deserted or active nests of *M. assumptionis* or *P. plumata*, nests of *D. distincta*, or any other sort of cavity. When they interrupt their flight, they may or may not stop near the cavity entrance, possibly entering as far as the level of the thorax or else com-

pletely. The time spent in a cavity varies and sometimes they are accompanied by a female who is already there, and in the morning sometimes they remain in the cavities for over an hour.

The males are able to patrol the whole of the trail extension; four individuals were located 600 m from where they had been marked. The scattered-nesting pattern influences the behavior of the males and might be one of the primary reasons for patrolling (Martins and Almeida 1994).

Males were often observed near the entrances of active nests, adopting a peculiar posture, which may be described as the "guard position". When in this posture, their wings were half-open or entirely closed. They would also perform a brief flight and then come back again soon afterwards. As this phenomenon was only observed in active nests, it can be explained by the presence of a female either provisioning or preparing the nest for provisioning.

Mating.—Matings were observed on the soil near the nest entrances and on flowers of *Vernonia rubriramea*. Although both sexes were promiscuous, up to 6 matings were observed for a single couple. Between one mating and the next, the male would visit flowers to drink nectar, as was seen once on a bush of *Waltheria americana* (Sterculiaceae).

The pattern of the mating process was as follows: the female remains inside the nest with the male standing in the 'guard position'. Then he enters up to the level of the thorax or half the body and probably touches the female abdomen before leaving the nest. Shortly afterwards, the female leaves too, and allows the male to mount her. He holds her body with his front legs and sometimes opens his wings before going away. Copulation lasts for about 3 seconds. Then, the female starts gathering pollen again. The male either disappears or else mates with another female in a nearby nest.

Not every male succeeds; sometimes the

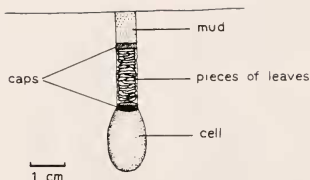


Fig. 1. Structure of a nest of *M. assumptionis*, in a deserted nest of *Ptilothrix plumata*, showing the closing "caps."

females did not allow them to approach, and even after the male had mounted, mating was not always finished because the female would fly away. When there were no females, the males would stay inside the active nests, only leaving when the resident female returned, to let them inside. Sometimes, while flying back to their nests, the females were followed by the males. On other occasions, the males would stay inside the nests, together with the females, for about one minute. There is no clear explanation for this behavior.

In *M. brevis*, males occasionally pursued the females and tried to approach them. However, not enough mating was observed during the three years of study for any definite conclusions to be drawn (Michener 1953). Apparently mating tended to occur very soon after emergence. By contrast, mating of *M. assumptionis* was observed throughout the reproductive season, with matings recorded in April (late), May (early), July (early), and August (early), and males present throughout the season.

Cell Construction and Provisioning.—After selecting a deserted nest, the female starts working in it, keeping the basic structure intact (Fig. 1). Cells averaged 1.55 ± 0.18 cm in height and 1.14 ± 0.06 cm in width and were linked to the outside by tunnels averaging 2.38 ± 0.55 cm in height and 0.50 ± 0.03 cm in diameter ($n = 6$). The female first lines the inner cell

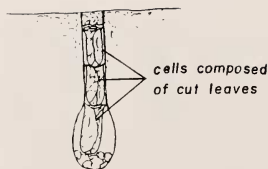


Fig. 2. Structure of the brood cells in a nest of *Megachile neoxanthoptera* in a deserted nest of *Ptilothrix plumata*.

wall, spreading a paste made of masticated leaves mixed with a presumed mandibular or salivary secretion. It is unknown whether the unusual clypeal horn of this species is used in the process. This results in a lining that eventually turns into a dry and darker thin material, hardly separable from the wall.

Due to their specialized behavior in using deserted nests of *P. plumata*, the cells of *M. assumptionis* do not follow the general pattern adopted by leaf cutter bees, as in *M. brevis* (Michener 1953), *M. neoxanthoptera* (Martins and Almeida 1994), or *M. instita* (Yanega 1994). Usually, these and other species of the same genus cut long pieces of leaves and/or petals to make brood cells in the form of an overlapped leaf structure, sometimes called a "cup", which is easily detachable (Fig. 2). These species also cut round pieces of leaves and petals to make the caps that block the nests'/cavities' entrances.

Megachile assumptionis does not utilize the free room available in the tunnel to construct more cells. This behavior differs from that of *M. neoxanthoptera*, which, for example, once occupied a deserted nest of *P. plumata*, with three cells placed end to end and snugly fitted (Fig. 2). In comparison, *M. brevis* may construct 1–11 cells, using all room available in the hollow (Michener 1953). After the cell has been lined, provisioning is started, the final product being a semisolid mass composed of pollen and nectar. A part of this mate-



Fig. 3. Closed nest entrance of *Megachile assumptionis*, showing the small pebbles used in the process and the intact turret.

rial comes from *Vernonia rubriramea* (Asteraceae) plants, where some females were observed gathering pollen and where bees of both sexes were seen drinking nectar. *M. brevis* uses a pollen and nectar mixture in provisioning its nests, as well (Michener 1953), as do all *Megachile* species.

When the provisioning has finished, the female lays an egg on top of the surface of the provision mass as in *M. brevis* (Michener 1953). The egg is about 5 mm long, with a similar shape but larger than that of *M. brevis*, which is 3 mm long.

Mature larvae of either species construct a cellophane-like waterproof cocoon that, in the case of *M. assumptionis*, helps preserve a favorable microhabitat during the period of immature dormancy (which is sometimes long; see below).

Nest Closure.—After laying the egg, the female blocks the cell entrance with a small cap, made of a mixture of chewed leaves, grains of sand and a secretion, probably glandular. Then she fills in the tunnel, just above the cell, with several layers of cut and overlapped leaves, that are pressed and compacted by the mandibles. As she cuts the leaves, the bee turns its body so that a piece is cut out with the mandibles working like scissors, in semicircular movements.

When the tunnel is filled in, the female leaves the nest, comes back with water, and then starts, close to the nest, to collect sand and/or pebbles. This material is gathered by the front legs and is then transferred to the mandibles, where it is mixed with water to produce mud. The pebbles are either obtained around the nest entrance, left over from *P. plumata* ex-

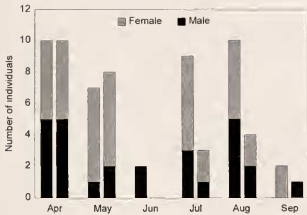


Fig. 4. Number of individuals of *Megachile assumptionis* marked in 1993 (gray bars) and 1994 (black bars).

cavation (Martins *et al.* 1996), or even taken from leaf-cutter ant colonies (*Atta* sp.). The female seems to push the mud by using her mandibles, and in this way constructs another cap, at ground level. The number of caps constructed in the nests could be 1–2. When there were 2 caps present, another layer made of cut leaves was found between them.

The process of nest closing might be interrupted by the female in order to get some nectar. This happened in the case of one female, which flew to one *V. rubrimea* close to her nest.

The last step in nest closure consists of gathering sand and/or pebbles with the mandibles and putting them together on top of the nest entrance (Fig. 3). In this process the bee avoids destroying the little turret (about 1.5 cm) constructed by the *P. plumata* female (Martins *et al.* 1996). This particular behavior of *M. assumptionis* makes clear the difference between her closed nests and those of *P. plumata*, whose females usually destroy the turret during nest closure (Martins *et al.* 1996).

Nesting Activity, Life Span and Dormancy.—*M. assumptionis* is a locally rare species, which makes generalizations on phenology difficult. However, observations on a total of 66 individuals in two consecutive years indicate activity from April to September (Fig. 4).

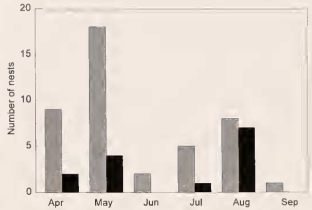


Fig. 5. Number of nests founded by *Megachile assumptionis* in 1993 (gray bars) and 1994 (black bars).

The adult population varies during the year with two peaks. The first one is in April and May and the second in July and August. During June and from September to March, the adults were hardly seen or not seen at all. For unknown reasons there was a steep fall in number between these two peaks in June in both years (Fig. 4).

During the active season, 43 and 14 nests were founded in 1993 and 1994 respectively (Fig. 5). The bees are more active from April to May and from July to August, with a sharp decrease in July and September (Martins and Almeida 1994). However, we found a smaller number of founded nests in the first portion of the second year as compared to the same time in the previous year (Fig. 4). This difference might be related to a reduced availability of nests of *P. plumata*: 404 in 1992, 275 in 1993 and 270 in 1994 (Martins *et al.* 1996). The decrease in the nesting activity might also have been due to environmental factors; drought might have made it difficult for the bees to dig their nests.

There is a time lag of 1 month between the peak of nests founded by *M. assumptionis* and *P. plumata*. This time lag in nest founding occurs because of the delay in adult emergence time resulting from *M. assumptionis* prepupal dormancy (Martins and Almeida 1994). *M. assumptionis* prepupae also become dormant throughout the rainy season, from October to January,

Table 1. Recorded emergences of *Megachile assumptionis* in 1993 and 1994.

Egg laying date	Nest number	Emergence date	Generation	Egg laying-emergence adults interval
27-04-1993	1	17-08-1993	2 nd	112
08-05-1993	2	23-08-1993	2 nd	107
09-05-1993	3	27-07-1993	2 nd	79
24-05-1993	4	05-08-1993	2 nd	73
05-07-1993	5	02-05-1993	1 st	302
07-07-1993	6	21-04-1993	1 st	289
16-08-1993	7	02-05-1993	1 st	260

when the first few nests are founded (Fig. 5). This dormancy can be interpreted as an adaptation or preadaptation of *M. assumptionis* which allows synchronization of the reproductive peaks between species. This synchronization is important for *M. assumptionis* reproduction because the number of available deserted nests was higher in the *P. plumata* nesting peak (Martins and Almeida 1994).

It was not possible to exactly determine the egg-adult developmental time. The reason for this is that upon reaching maturity, the larvae can halt development and stay in diapause as prepupae. However, it was possible to record the time between egg laying and the emergence of adults and make observations of the time of 7 emergences (Table 1). These intervals were either about 9 months (5–7) or 2 to 3 months (1–4).

The adult emergence pattern ($n = 7$) confirms that there are at least two generations per year (Table 1). The first one is represented by the progeny of the last individuals from the previous year, which remain dormant for about 9 months. Three emergences were recorded from April to May in 1994 and they correspond to nests founded in July and August in 1993. The second generation was characterized by four emergences recorded in July and August in 1993, which correspond to nests founded in April and May of the same year. Individuals of this sec-

Table 2. Mortality, survival and desertion of nests in *Megachile assumptionis* in 1993 and 1994 (percentage in parentheses).

Nest status	Number of nests	
	1993	1994
Marked	43	14
Deserted	1	2
Founded	42 (100)	12 (100)*
Lost	12 (29)	—
Survival	11 (26)	5 (50)
Mortality	19 (45)	5 (50)

* Two nests from 1994 were left in the field.

ond generation remain in dormancy for 2–3 months. On the other hand, we found one larva that had been dormant for about 7 months, in one nest founded in April 1993 that was excavated in October of the same year. This indicates a possible variability in larval developmental time, as recorded for other temperate megachilid species, called parsivoltinism by Torchio and Tependino (1982). Additionally, in species of other megachilid genera, *Prochelostoma*, *Osmia* and *Hoplitis*, a period of 2 years in dormancy has been observed (Danks 1987), indicating that *M. assumptionis* may possibly have the ability to remain in dormancy for longer than the 9 months recorded. This suggests that wide variability in emergence times recorded for other solitary bees and wasps should also be common at seasonal tropical sites (Martins *et al.* 1996; Martins unpublished data).

Survival and mortality rates were calculated from emergence and nest excavation data. Twenty-three nests were excavated in 1993 and 10 nests in 1994, with all nests containing dead individuals, mold, or lacking evidence of successful brood considered as dead and excavated nests which contained pupae or healthy larvae considered successful.

Discounting the number of lost nests, the mortality rate was 45% in 1993 and 50% in 1994 (Table 2). The causes of the high immature mortality rate are un-

known. In at least 17% of the excavations there was no sign of any cell, tunnel or immatures. Furthermore, in 1993, 12 nests were lost due to work done by a bulldozer in the study area. According to Martins *et al.* (1996), one possible reason for the loss of the contents of bee nests is ground modifications resulting from termite activity or even the intense predation by ants nesting in the vicinity.

Diptera rather than termites are more commonly known as natural enemies of solitary bees. Among them, larvae of *Anthrax* sp. (Bombyliidae) have previously been observed consuming *Megachile* larvae (Roubik 1989). Although species of *Anthrax* occurred in the nesting site of *M. assumptionis* and were recorded parasitizing *P. plumata* nests (Martins *et al.* 1996), no individuals emerged from any of the *M. assumptionis* nests. This might be partially due to parasite preference for another apid, *Diadasina distincta*, that nests in the same area and is heavily parasitized (Martins and Antonini 1994).

Adult Longevity and Mobility.—The recovery rate of marked bees was 45%. These figures are satisfactory when compared to those found for *M. brevis*—8% (Michener 1953). The low numbers found by this author are accounted for by the remarkable mobility of the individuals. The bees would concentrate in an attractive patch of flowers and then disperse when they ceased to bloom. The result was an apparent drop in the population size (Michener 1953). In contrast, *M. assumptionis* individuals were more sedentary, since they were locally confined to the nesting site of *P. plumata*. In 1994, for example, all recoveries occurred in the same place where the bees had been marked, indicating low mobility (Martins and Almeida 1994).

The data recorded for *M. assumptionis* show male bees may live about twice as long as females. In both years, the individuals were recovered between 2 to 48 days after being marked. In 1993, the maximum

values observed were 48 days for a male and 19 days for a female. In 1994, the values recorded were 28 days for a male and 16 days for a female. As regards *M. brevis*, the maximum time interval between the marking and the recovery was 22 days for a male, although there is some evidence to suggest that the individuals can live for approximately one month (Michener 1953).

This also suggests that longevity in individuals of tropical solitary bee species can be longer than in temperate regions, but much more data on other species is needed to verify this possibility, as there is a lack of information (Roubik 1989).

CONCLUSION

The behavior and nesting dynamics of *M. assumptionis* show that it is a rare species in this locality and specialized in that it uses deserted nests of *P. plumata*. Unlike most of the species in the genus whose nesting biology is known, *M. assumptionis* does not construct rows of brood cells of cut leaf pieces in natural cavities or burrows of its own making, but instead uses the pre-existing, empty cells constructed by another solitary bee, provisioning only a single cell in each nest. It may therefore experience a scarcity of suitable nesting sites and some restrictions on fecundity, and we suppose that the limiting resource in the ecology of this species is nest sites rather than pollen availability or predator/parasite pressure. In contrast, *M. brevis* is one of the commonest *Megachile* species in North America, presumably because it is so generalized in its use of nesting substrates.

ACKNOWLEDGMENTS

Frank Hanson, Doug Yanega and Fernando Silveira made helpful comments on this manuscript. Charles Michener identified *M. assumptionis* and *P. plumata*. Arturo Roig-Alsina identified *D. distincta* and Pe. J. Moure identified *M. neoxanthoptera*. The late Hermogenes F. Leitão Filho identified *V. rubriramea* and *W. americana*. We thank the zoologist Myrian M. Duarte for the drawings and Sidnei T. M. Guerra,

Hélcio R. Pimenta and Lourdes Aragão Soares for the help in the field and in the lab. The Brazilian CNPq and FAPEMIG conceded a grant to R. P. Martins and a scholarship for R. P. Martins and D. A. O. Almeida. This study is a contribution of the Program in Ecology, Conservation and Wildlife Management of the Universidade Federal de Minas Gerais, Belo Horizonte, Brazil.

LITERATURE CITED

- Batra, S. W. T. 1984. Solitary bees. *Scientific American* 259: 120-127.
- Bohart, G. E. and N. N. Youssef. 1972. Notes on the biology of *Megachile* (*Megachiloides*) *umatillensis* Mitchell (Hymenoptera: Megachilidae) and its parasites. *Transactions of the Royal Entomological Society of London* 124(1): 1-19.
- Danks, H. V. 1987. *Insect dormancy: an ecological perspective*. Biological Survey of Canada (Terrestrial Arthropods). 439 pp.
- Eickwort, G. C., R. W. Matthews and J. Carpenter. 1981. Observations on the nesting behavior of *Megachile rubi* and *M. texana* with a discussion of the significance of soil nesting in the evolution of megachilid bees (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 54(3): 557-570.
- Iwata, K. 1976. *Evolution of instinct: comparative ethology of Hymenoptera*. Amerind Publishing Co. Pvt. Ltd. New Delhi, India.
- Krombein, K. 1967. *Trap-nesting wasps and bees: Life histories, nests, and associates*. Smithsonian Press, Washington, D. C. 570 pp.
- Martin, P. and P. Bateson. 1993. *Measuring behavior*. Cambridge University Press, Cambridge. 222 pp.
- Martins, R. P. and J. E. C. Figueira. 1992. Spatial distribution of nests in *Diadasina distincta* (Holmberg) (Hymenoptera: Anthophoridae). *Journal of Insect Behavior* 5(4): 527-529.
- Martins, R. P. and D. A. O. de Almeida. 1994. Is the bee *Megachile assumptionis* a cavity-nesting specialist? *Journal of Insect Behavior* 7(5): 759-765.
- Martins, R. P. and Y. Antonini. 1994. The biology of *Diadasina distincta* (Holmberg) (Hymenoptera: Anthophoridae). *Proceedings of the Entomological Society of Washington* 96(3): 553-560.
- Martins, R. P., F. G. Guimarães and C. M. Dias. 1996. Nesting biology of *Ptilothrix plumata* Smith, with a comparison to other species in the genus (Hymenoptera: Anthophoridae). *Journal of the Kansas Entomological Society* 69(1): 9-16.
- Messer, A. C. 1984. *Chalicodoma pluto*: The world's largest bee rediscovered living communally in termite nests (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 57: 165-168.
- Michener, C. D. 1953. The biology of the leafcutter bee (*Megachile brevis*) and its associates. *The University of Kansas Science Bulletin* 35(16): 1659-1748.
- Michener, C. D. 1974. *The social behavior of the bees*. Harvard University Press, Cambridge, MA. 404 pp.
- Michener, C. D. and J. J. H. Szent-Ivany. 1960. Observations on the biology of a leaf-cutter bee "*Megachile frontalis*," in New Guinea. *Papua and New Guinea Agricultural Journal* 13: 22-35.
- Roubik, D. W. 1989. *The ecology and natural history of tropical bees*. Cambridge Tropical Biological Series, Cambridge University Press, Cambridge. 514 pp.
- Sakagami, S. F., S. Laroca and J. S. Moure. 1967. Wild bee biocoenotics in São José dos Pinhais (PR). South Brazil. Preliminary report. *Journal of the Faculty of Agriculture Hokkaido University, Series VI, Zoology* 16: 253-271.
- Stephen, W. P., G. E. Bohart and P. F. Torchio. 1969. *The biology and external morphology of bees*. Agricultural Experimental Station, Oregon State University, Corvallis, OR. 140 pp.
- Torchio, P. F. and V. J. Tepedino. 1982. Parsivoltinism in three species of *Osmia* bees. *Psyche* 89(3-4): 221-238.
- Yanega, D. 1994. Nests and hosts of three species of megachilid bees (Hymenoptera: Apoidea: Megachilidae) from Coahuila, México. *Journal of the Kansas Entomological Society* 67: 415-417.